

Research Article

# Changes in species and phylogenetic diversity in tropical seasonal rainforests on steep karst hillslopes in southwestern China: implications for conservation

Qingling Pang<sup>1\*</sup>, Cong Hu<sup>1\*</sup>, Chaohao Xu<sup>1</sup>, Chaofang Zhong<sup>1</sup>, Zhonghua Zhang<sup>1,2,3</sup>, Gang Hu<sup>1,2,3</sup>

<sup>1</sup> Key Laboratory of Environment Change and Resources Use in Beibu Gulf, Ministry of Education, Nanning Normal University, Nanning 530100, China

<sup>2</sup> Guangxi Key Laboratory of Earth Surface Processes and Intelligent Simulation, Nanning Normal University, Nanning 530100, China

<sup>3</sup> Key Laboratory of Wildlife Evolution and Conservation in Mountain Ecosystem of Guangxi, Nanning Normal University, Nanning 530100, China

Corresponding authors: Zhonghua Zhang ([zzh@nnnu.edu.cn](mailto:zzh@nnnu.edu.cn)); Gang Hu ([hugang@nnnu.edu.cn](mailto:hugang@nnnu.edu.cn))

## Abstract

Tropical karst seasonal rainforests (TKSR) in southwestern China have high levels of biodiversity and a significant number of endemic species. However, understanding the distribution of plant diversity and the mechanisms driving community assembly in these diverse and heterogeneous karst forests remains limited. This study examined the species and phylogenetic diversity of the herb, shrub, and tree layers in the TKSR along steep hillslopes within karst peak-cluster depressions in southwestern China. Species richness in the herb, shrub, and tree layers showed an inverted U-shape pattern, with richness lower in the middle and higher on the sides of the hillslope. The upper slope had a higher level of species richness than the depressions and the lower and middle slopes. The phylogenetic structures of the herb and tree layers tended to be clustered, whereas the shrub layer exhibited a divergent phylogenetic structure. These findings indicate that community assembly in the TKSR is influenced by habitat filtering and competitive exclusion. Soil total phosphorus (STP) and soil available phosphorus (SAP) were identified as significant factors affecting species diversity across the three layers, whereas the rock outcrop rate was a significant factor affecting the phylogenetic structure. In the shrub and tree layers, STP and SAP were important determinants of phylogenetic diversity. These results highlight the impact of environmental heterogeneity on species and phylogenetic diversity in the TKSR. Furthermore, depressions and upper slopes with high species and phylogenetic diversity were identified as priority areas for conservation in the karst peak-cluster depressions of southwestern China.

**Key words:** Community assembly, karst forest, phylogenetic structure, plant diversity, slope position



Academic editor: Ilona Blinova

Received: 19 June 2025

Accepted: 12 October 2025

Published: 4 November 2025

ZooBank: <https://zoobank.org/FDBA1FC3-45CC-4410-8568-B24703AF42A6>

**Citation:** Pang Q, Hu C, Xu C, Zhong C, Zhang Z, Hu G (2025) Changes in species and phylogenetic diversity in tropical seasonal rainforests on steep karst hillslopes in southwestern China: implications for conservation. *Nature Conservation* 60: 73–97. <https://doi.org/10.3897/natureconservation.60.162595>

Copyright: © Qingling Pang et al.  
This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

## Introduction

Changes in plant diversity along environmental gradients are important in the field of vegetation ecology (Liu 2017). Slope, as a topographical factor, plays a crucial role in controlling the spatial distribution of water, light, heat, and soil nutrients, and influences the abundance, distribution, and diversity of vegetation in mountainous

\* These authors contributed equally to this work.



and hilly areas (Zeng et al. 2014). Plant diversity patterns along slopes often exhibit complex and non-monotonic changes that are closely related to topography, water, and heat conditions, as well as various life forms, including trees, shrubs, and herbs (Deák et al. 2021; Sharma and Kala 2022). Many studies have investigated the impact of slope on vegetation in various ecosystem types (Zeng et al. 2014; Berry et al. 2016; Zhang et al. 2020; Dong et al. 2022; Liang et al. 2024). Understanding plant diversity patterns along slopes and the underlying mechanisms is crucial to elucidating the relationship between vegetation and the environment.

Species diversity is a central aspect of biodiversity and ecology research, reflecting community structure, developmental stages, stability, and habitat differences, and can also reveal the organizational levels of plant communities (Li et al. 2019). Understanding the influence of environmental factors on species diversity is an important ecological question (Weigel et al. 2019). Plant communities are typically composed of species with various life histories that occupy distinct ecological niches (Nettesheim et al. 2018). As the community environment changes, the niches occupied by these species can change, leading to different patterns of heterogeneity in the community (Bagaria et al. 2019). Consequently, different communities often exhibit differences in species composition, structure, and functional traits; elucidating these differences is crucial to understanding how species diversity varies across different environments (Geng et al. 2022). Phylogenetic diversity can be used to assess the uniqueness of biological taxa in specific spatiotemporal contexts based on the evolutionary history of the species. It is also indicative of biodiversity conservation because it can be used to identify phylogenetic relationships and evolutionary information among different species (Chen et al. 2021). Phylogenetic structures complement phylogenetic diversity and can be used to infer the ecological processes affecting community assembly. When integrated, the composition, origin, and evolutionary processes of species can be explored from both evolutionary and ecological perspectives, thereby promoting the rational conservation of plant diversity (Ci and Li 2017). Phylogenetic diversity interprets a species' evolutionary history from a phylogenetic relationship perspective. When combined with species diversity, it greatly enhances our understanding of population dynamics and ecological niche differentiation (Zeng et al. 2014), providing a new perspective for biodiversity conservation. Although previous studies have focused on species patterns and phylogenetic diversity in different forest types worldwide (Myers et al. 2013; Qian et al. 2014; Yang et al. 2014; Guo et al. 2018; Gastauer et al. 2020), understanding of vegetation distribution characteristics in special landforms, such as karst landscapes, remains limited.

Karst landscapes are formed by the effects of rainfall and groundwater on carbonate bedrock (De Waele 2017). These landscapes are widespread, occurring on approximately 15%–20% of the Earth's ice-free land surface, with the largest continuous area spanning roughly 0.51 million km<sup>2</sup> in southwestern China (Jiang et al. 2014). Owing to their high sensitivity and vulnerability, the conservation of biodiversity in karst areas is of great importance (Sun et al. 2020). Karst areas in southwestern China are recognized as one of the 25 global biodiversity hotspots because of their unique biomes. The distinctive landforms they create consist of peak-cluster depressions, characterized as closed and flat depressions surrounded by a series of hills. Karst peak-cluster depressions contribute to the complexity and diversity of landforms in karst areas (Yang et



al. 2014) and display rapidly changing topographical characteristics, transitioning from cliffs to depressions over short horizontal distances. In addition, the potential energy decreases dramatically from the top slope to the depression area, resulting in a significant potential gradient. These peak-cluster depressions provide the topographic and hydrological conditions necessary for the development of a catenary pattern of soil and vegetation (Meng et al. 2022). Karst peak-cluster depressions in southwestern China are generally at low elevations (between 200 and 500 m) but often exhibit steep slopes (greater than 30°). In these areas, elevation is not considered the primary factor influencing species diversity in communities, especially in low- and small-scale regions (Zeng et al. 2014). Slope position has been recognized as one of the major topographic factors that determine microclimates and ecological niches for species in karst mountain regions, as it influences various aspects such as sunlight, soil depth, soil moisture, and nutrient availability (Gong et al. 2008; Weintraub et al. 2015).

Mountainous and hilly areas encompassing steep environmental gradients in small geographic areas are outstanding natural laboratories for biodiversity studies because numerous environmental factors, such as temperature (Wu et al. 2013), productivity (Ramírez-Bautista and Williams 2019), and anthropogenic disturbance (Santillán et al. 2020), can correlate with elevation and consequently exert effects on biological communities. Along slope position gradients, karst peak-cluster depressions exhibit highly heterogeneous microhabitats due to variations in multiple environmental factors, resulting in significant differences in biodiversity. For example, Peng et al. (2019) reported that slope was the major driver of the spatial distribution of soil microbial richness and diversity in a karst forest due to its effects on plant characteristics (i.e., tree Shannon diversity and tree density) and soil properties (i.e., soil pH and available phosphorus). Similarly, Sun et al. (2020) revealed spatial incongruence among the taxonomic, functional, and phylogenetic diversity of small mammals along elevation gradients in karst mountains. Other studies have focused on variations in soil physicochemical properties and plant–litter–soil ecological stoichiometry along slope position gradients in karst peak-cluster depressions (Zeng et al. 2015; Chen et al. 2019; Hu et al. 2020). However, it remains unclear how plant species and phylogenetic diversity change along slope position gradients in karst peak-cluster depressions and the driving factors behind these changes.

The Nonggang National Nature Reserve in southwestern China is a representative of karst peak-cluster depression landforms worldwide. The tropical karst seasonal rainforests (TKSR) in this reserve are characterized by complex structures, rich species composition, and prominent endemic elements. This area is also one of the 14 key areas of terrestrial biodiversity of international significance in China (Huang et al. 2013). Thus, the TKSR is irreplaceable and significant for the restoration and protection of karst forest ecosystems (Zeng et al. 2023). Recent ecological studies on the TKSR have focused on species composition, spatial distribution, and diversity (Ma et al. 2023). Studies have found that the diversity of woody plant species in the TKSR is unimodal, but there is also a bimodal pattern that increases with elevation, and the diversity pattern is strongly influenced by topographic heterogeneity (Huang et al. 2016). Furthermore, Guo et al. (2017, 2018) investigated the effects of deterministic and stochastic processes on community assembly in the TKSR at a 15-ha plot scale and found that both processes play important roles. Although it is recognized that topography influences the spa-



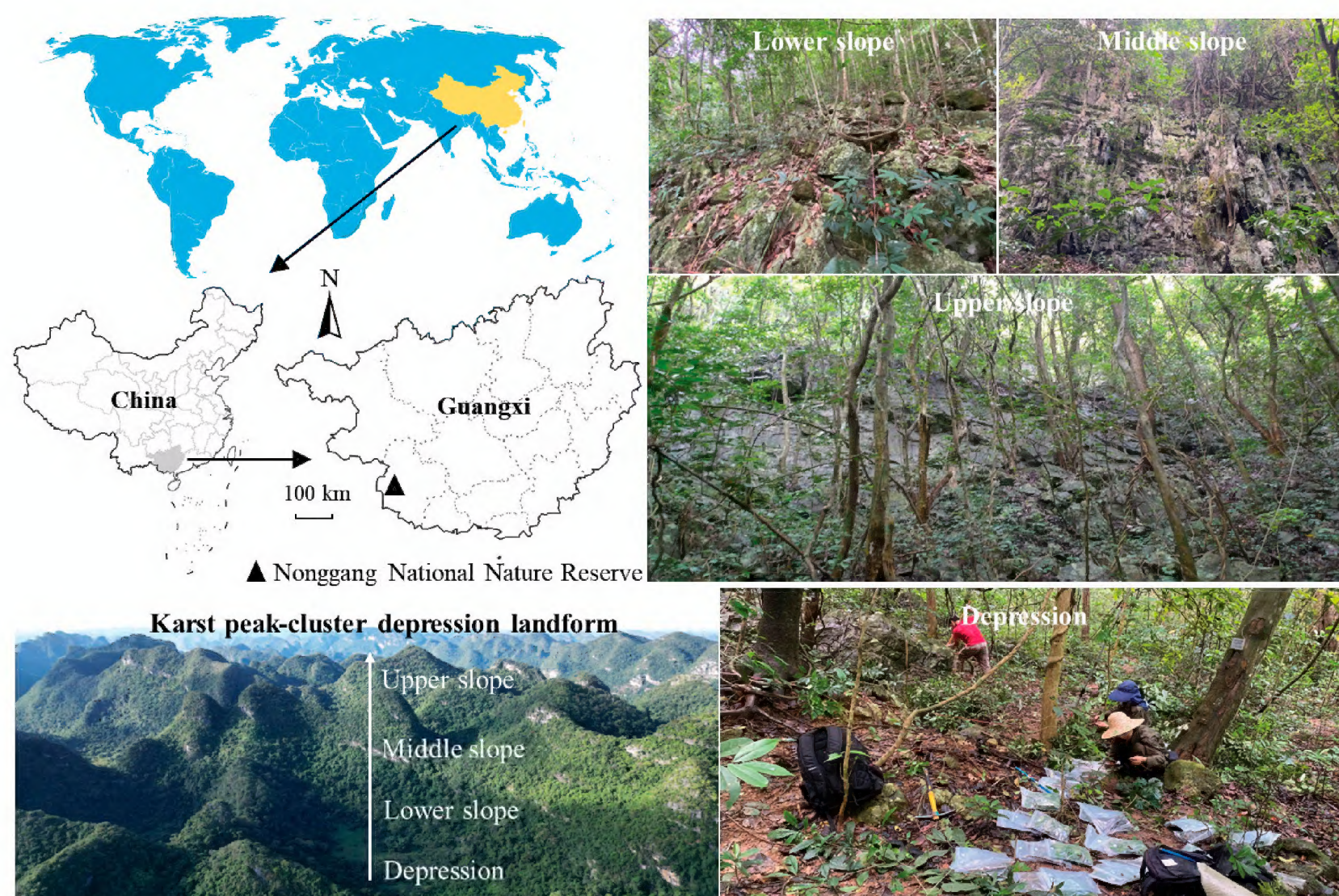
tial distribution of trees in the TKSR, the dominant biotic and abiotic factors that affect the distribution patterns of species and phylogenetic diversity remain unclear.

In this study, plot surveys and environmental factor measurements were conducted in the TKSR of the Nonggang National Nature Reserve with a focus on different slopes (depression, lower slope, middle slope, and upper slope). Gradient changes in community species and phylogenetic diversity across three forest strata (herb, shrub, and tree layers) and the factors influencing these changes were examined. The objective of this study was to reveal (1) the spatial patterns of species diversity, phylogenetic diversity, and structure within slope gradients in the herb, shrub, and tree layers and (2) the primary environmental factors influencing these spatial patterns. The results provide a scientific basis for improving understanding of forest community structure, ecosystem functions, and ecological conservation in karst peak-cluster depressions.

## Materials and methods

### Study area

The Nonggang National Nature Reserve, located in the southern Guangxi Zhuang Autonomous Region, southwestern China ( $22^{\circ}13'56''$ – $22^{\circ}39'09''$ N,  $106^{\circ}42'28''$ – $107^{\circ}04'54''$ E; Fig. 1), covers an area of 10,080 ha. The region has a tropical monsoon climate, with an average annual temperature of approximately 22 °C. The temperature ranges from above 13 °C in January, the coldest month, to above 28 °C in July, the hottest month. The annual accumulated temperature ranges from 7,400 to 7,800 °C. Annual average rainfall ranges from 1,200 to 1,500 mm and is concentrated between May and September. The bedrock of the area is primarily



**Figure 1.** Geographical location of the study area, with photographs showing tropical karst seasonal rainforests along steep karst hillslopes.



composed of limestone, and the main soil types are primitive calcareous, brown calcareous, and black calcareous. The topography of the region is characterized by typical karst peak-cluster depression landforms, with depressions formed by clustered peaks sharing a common base and a funnel-shaped landscape. Elevation ranges from 150 to 600 m. Unique landforms, such as peak clusters, forests, depressions, and funnels, result in significant variations in light availability, soil thickness, and moisture. Other micro-landform features formed by numerous rock outcrops—such as stone gullies, stone surfaces, and depressions—contribute to the heterogeneity of small-scale habitats. The reserve contains 1,752 recorded species of vascular plants belonging to 810 genera and 184 families (Huang et al. 2013). Among these, 33 species are rare and endangered in China, and 278 species are endemic to karst habitats (Wang et al. 2014). The dominant tree species in the TKSR include *Excentrodendron tonkinense* (A. Chev.) H.T. Chang & R.H. Miao, *Camellia petelotii* (Merr.) Sealy, *Cephalomappa sinensis* (Chun & F.C. How) Kosterm., *Garcinia paucinervis* Chun ex F.C. How, and *Deutzianthus tonkinensis* Gagnep.

## Data collection

During the peak growing season from July to September 2020, forest plots were established at different slope positions based on elevation variations in the karst peak-cluster depressions in the study area (Fig. 1). There were 10 plots, each with an area of 20 × 20 m, at four slope positions—depression (DE), lower slope (LS), middle slope (MS), and upper slope (US)—with a spacing of more than 30 m between plots. A total of 40 plots were established along steep karst hillslopes in the study area. Tree-layer investigations included species names, diameters at breast height (DBH), and heights. Within each plot, two 5 × 5 m subplots were randomly established to investigate the shrub layer, including species names, average heights, coverages, and numbers. Additionally, four 1 × 1 m subplots were randomly established to investigate the herb layer, including species names, numbers, heights, and coverages. All vascular plants in each plot and subplot were inventoried, with species identifications verified by two plant taxonomy experts. Furthermore, latitude and longitude coordinates, elevation, aspect, slope position, and rock outcrop rate were recorded. Three experienced observers visually estimated the slope position and rock outcrop rate, and a handheld GPS (Garmin GPSMAP 60CSx) was used for all other measurements. Slope positions were represented by categorical variables 1, 2, 3, and 4, corresponding to depression, lower slope, middle slope, and upper slope, respectively (Qiu and Zhang 2000). The slope aspect was converted from a range of 0–360° azimuth to a value ranging from 0 to 1 using a previously documented formula (Yu et al. 2013).

Within each plot, soil samples were collected at depths of 0–20 cm using the five-point sampling method (Lu et al. 2023). The collected soil samples were mixed and returned to the laboratory. After air-drying and sieving, the soil samples were subjected to chemical analyses to determine various soil parameters. The measured indicators included soil pH, exchangeable calcium (ECa), exchangeable magnesium (EMg), available phosphorus (AP), available potassium (AK), ammonium nitrogen ( $\text{NH}_4^+\text{-N}$ ), nitrate nitrogen ( $\text{NO}_3^-\text{-N}$ ), organic matter (SOM), total nitrogen (TN), total phosphorus (TP), and total potassium (TK). Soil pH was determined in a suspension with a 1:2.5 soil-to-water ratio. ECa and EMg were measured using atomic absorption spectrophotometry (AA-7000, Shimadzu,



Kyoto, Japan).  $\text{NH}_4^+\text{-N}$  was quantified using the indophenol blue colorimetric method, and  $\text{NO}_3^-\text{-N}$  was measured using the cadmium reduction method followed by a sulfanilamide–NAD reaction. SOM content was determined using the traditional potassium dichromate oxidation method. TN was measured using the semi-micro Kjeldahl method. AP and TP levels were determined using the molybdenum–antimony colorimetric method. AK and TK levels were measured using the sodium hydroxide fusion flame photometry method. The surface soil water content (SWC) of each plot was measured using a portable three-parameter soil tester (WET-2, Delta-T Devices Ltd., United Kingdom) following the five-point sampling method (Lu et al. 2023). These methods for measuring soil properties were described in detail by Lu (1999) and Bao (2000). Environmental variables (mean  $\pm$  SD) in four slope positions are presented in Suppl. material 1: table S1.

## Data analysis

### Species diversity

The plant species names, along with their family and genus information within the study plots, were verified according to the APG III system using the *plantlist* package (Zhang 2018). Species richness ( $S$ ), Simpson index ( $D$ ), Shannon–Wiener index ( $H$ ), and Pielou index ( $J$ ) were calculated to assess species diversity in the plant communities (MacDonald et al. 2017). These indices were computed using the *vegan* package in R version 4.2.2 (Oksanen et al. 2019). The formulae used for the calculations are as follows:

$$D = 1 - \sum_{i=1}^S P_i^2 \quad (1)$$

$$H = - \sum_{i=1}^S P_i \cdot \ln P_i \quad (2)$$

$$J = H / \ln S \quad (3)$$

where  $S$  represents the species richness within the community plot and  $P_i$  represents the importance value of species  $i$  in the community.

### Phylogenetic structure and diversity

A phylogenetic tree of vascular plants was constructed using the *V.PhyloMaker* package (Jin and Qian 2019), incorporating evolutionary branch lengths based on the “GBOTB.extended.tre” framework following the methodological approach of scenario S3. This scenario employs average distances to constrain phylogenetic tip positions, thereby reducing bias introduced by polytomies. The “GBOTB.extended.tre” tree integrates the evolutionary branches of seed plants from GBOTB (Smith and Brown 2018) and ferns from the updated, revised, and expanded phylogenetic system of Zanne et al. (2014).

The Faith Diversity Index (PD) was used to measure phylogenetic diversity (Faith 1992). The net relatedness index (NRI) and nearest taxon index (NTI) were used to determine the phylogenetic structure. NRI and NTI represent the standardized values of the mean pairwise distance (MPD) and mean nearest taxon distance



(MNTD), respectively. The NRI primarily describes the overall phylogenetic relationships among species in a community, whereas the NTI focuses on phylogenetic relationships at the terminal branches of the phylogenetic tree. Compared with NRI, NTI places greater emphasis on describing the phylogenetic distances between neighboring species (Webb et al. 2002). MPD and MNTD were calculated using the `comdist` and `comdistnt` functions in the `picante` package (Kembel et al. 2008). The actual values for each community were compared using an unconstrained null model (Kembel and Hubbell 2006), in which the terminal branches of the phylogenetic tree were randomly permuted 999 times for all species in the community. The differences were then calculated, and the NRI and NTI values for each community were obtained (Webb et al. 2002; Swenson et al. 2007).

$$PD = \sum L_b \quad (4)$$

$$NRI = -1 \times \frac{MPD_{\text{observed}} - MPD_{\text{randomized}}}{sdMPD_{\text{randomized}}} \quad (5)$$

$$NTI = -1 \times \frac{MNTD_{\text{observed}} - MNTD_{\text{randomized}}}{sdMNTD_{\text{randomized}}} \quad (6)$$

where  $L_b$  represents the branch length connecting the species on the tree.  $MPD_{\text{observed}}$  and  $MNTD_{\text{observed}}$  are the observed values of the average pairwise phylogenetic distance and mean nearest taxon distance, respectively, for each plot.  $MPD_{\text{randomized}}$  and  $MNTD_{\text{randomized}}$  are the average pairwise phylogenetic distance and mean nearest taxon distance, respectively, obtained by randomly generating null models for the community.  $sdMPD_{\text{randomized}}$  and  $sdMNTD_{\text{randomized}}$  are the standard deviations of the average pairwise phylogenetic distance and mean nearest taxon distance obtained from the randomly generated null models for the community, respectively. If the NRI (or NTI)  $> 0$ , the phylogenetic relationships among individuals in the community are closer than those expected from a randomly generated null model, suggesting phylogenetic clustering. Conversely, if the NRI (or NTI)  $< 0$ , it suggests phylogenetic overdispersion, indicating that the phylogenetic relationships among individuals in the community are more divergent than expected from the null model (Webb et al. 2002). If the NRI (or NTI)  $< -1.96$ , it indicates significant phylogenetic evenness compared with the null model, whereas an NRI (or NTI)  $> 1.96$  indicates significant phylogenetic clustering compared with the null model (Vamosi et al. 2009).

## Statistical analysis

Assuming that the data were normally distributed and satisfied the assumption of homogeneity of variances, one-way ANOVA was used to compare differences in environmental variables among the different slope positions. For multiple comparisons of plant diversity between slope positions, the least significant difference (LSD) method was applied if variances were equal; however, if variances were not equal, the Games–Howell test was used. Pearson correlation analysis was conducted to examine relationships between species, phylogenetic diversity, and environmental variables. Factors with  $r > 0.6$  were removed. The remaining factors were then included in multiple stepwise regression analyses, along with diversity indices and phylogenetic structures, to identify the main

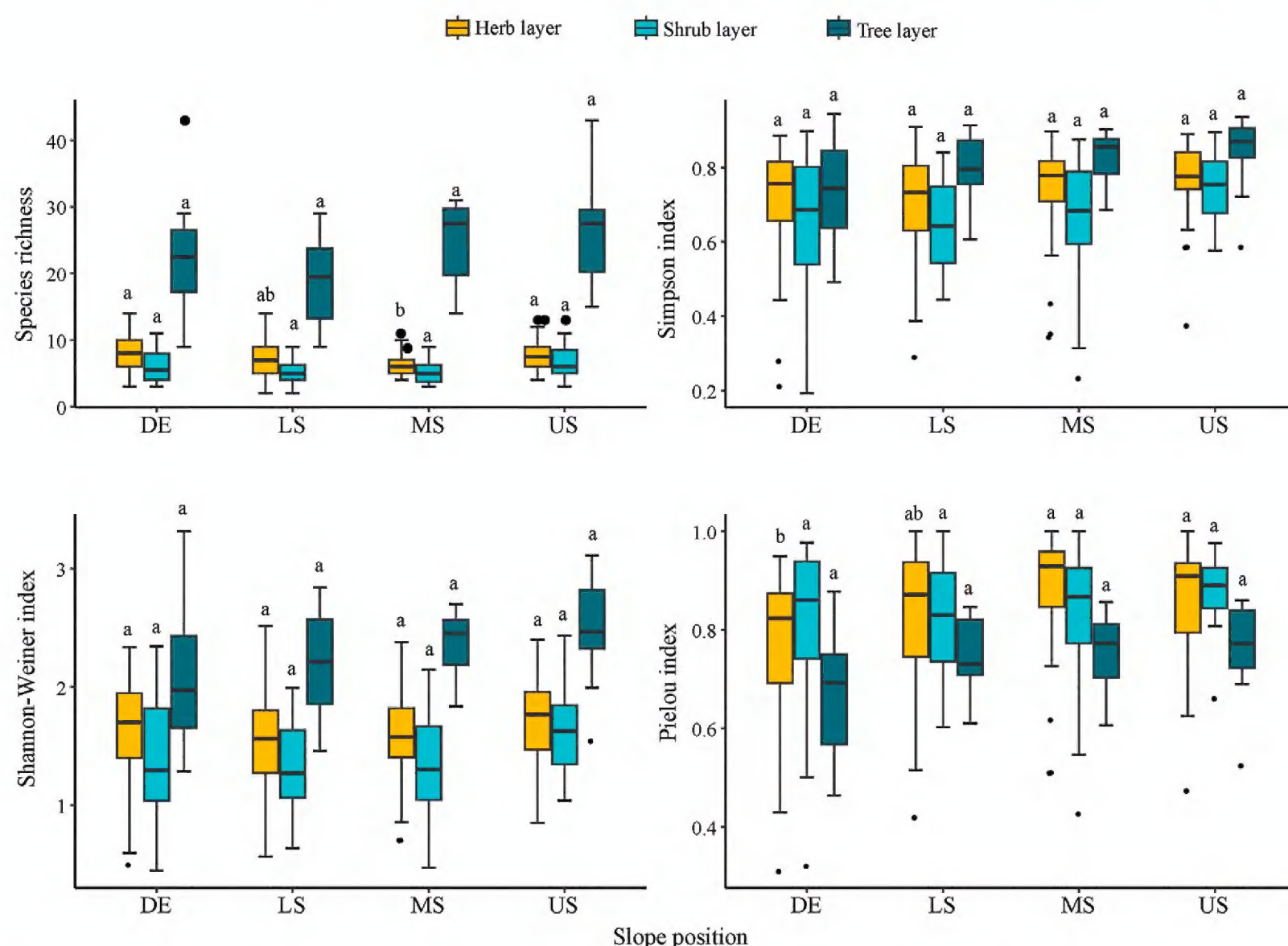


factors influencing species and phylogenetic diversity. The stepwise regression procedure was based on the Akaike Information Criterion (AIC), in which variables were added or removed by selecting the model with the minimum AIC value. Residual analysis confirmed that the model satisfied the assumptions of normality, linearity, and homoscedasticity, thereby validating the use of a regression model based on the Gaussian distribution. The factors retained in the regression equations were quantified using the *rdacca.hp* package (Lai et al. 2022) in R 4.2.2 to determine their explanatory power for the diversity indices through hierarchical partitioning analysis. One-way ANOVA and Pearson correlation analysis were performed using SPSS 26.0 (SPSS Inc., Chicago, IL, USA).

## Results

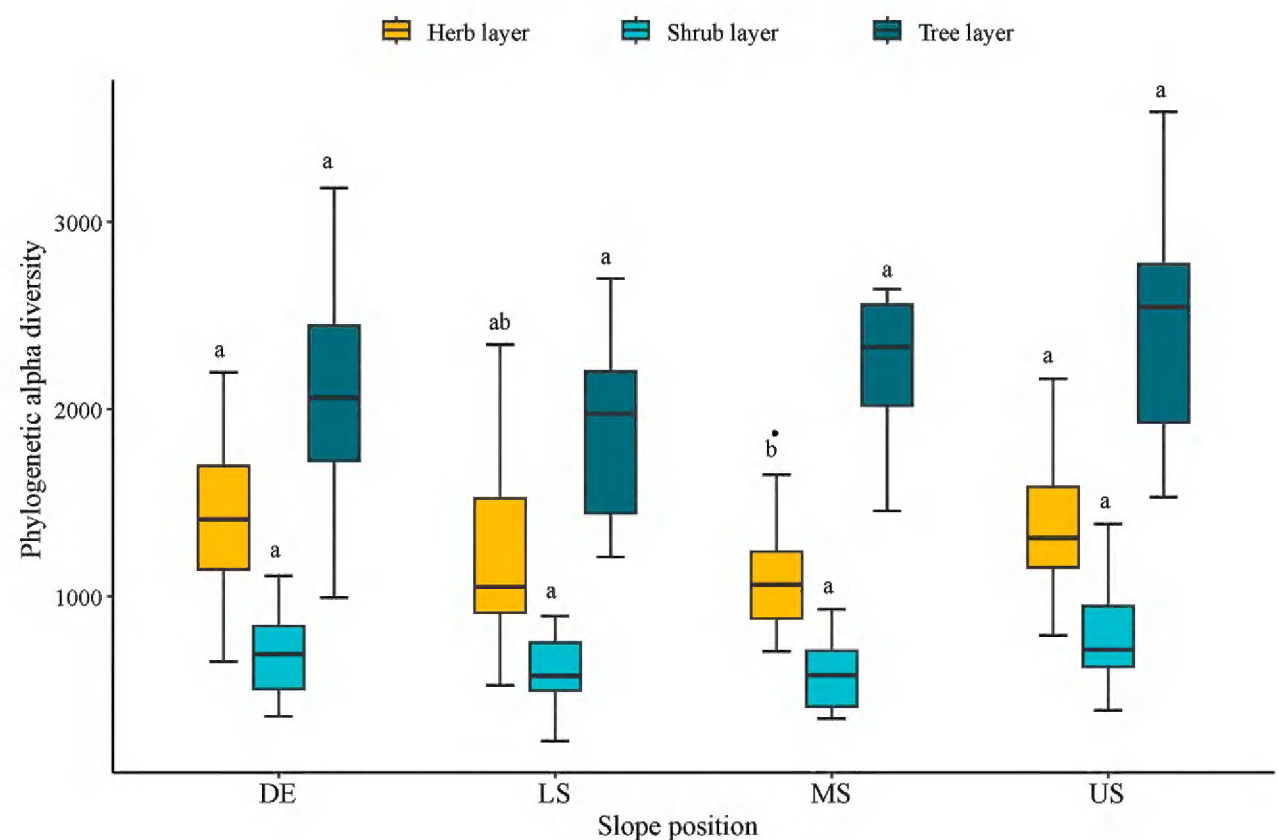
### Species and phylogenetic diversity at different slopes

Species diversity in the herb, shrub, and tree layers initially decreased and then increased with slope position (Fig. 2). In the herb layer, species richness in the middle slope was significantly lower than that in the lower and upper slopes ( $p < 0.05$ ), and the Pielou index showed an increasing trend, with values for both the middle and upper slopes significantly higher than those in the lower slopes ( $p < 0.05$ ). There were no significant differences in species diversity in the shrub layer among the different slope positions. In the tree layer, species richness initially decreased and then increased with slope position, whereas the other indices showed an overall increasing trend, with no significant differences among slope positions.



**Figure 2.** Changes in species diversity at different slope positions. Different lowercase letters indicate a significant difference between communities at different slope positions ( $p < 0.05$ ). DE, depression; LS, lower slope; MS, middle slope; US, upper slope.





**Figure 3.** Phylogenetic diversity at different slope positions. Different lowercase letters indicate a significant difference between communities at the various slope positions ( $p < 0.05$ ). DE, depression; LS, lower slope; MS, middle slope; US, upper slope.

Phylogenetic diversity in the herb, shrub, and tree layers initially decreased and then increased with slope position (Fig. 3). Specifically, phylogenetic diversity in the lower and upper slopes was significantly higher than that in the middle slope in the herb layer ( $p < 0.05$ ). In contrast, there were no significant differences in phylogenetic diversity among slope positions in the shrub and tree layers. Across the three layers, phylogenetic diversity was highest in the tree layer, followed by the herb and shrub layers.

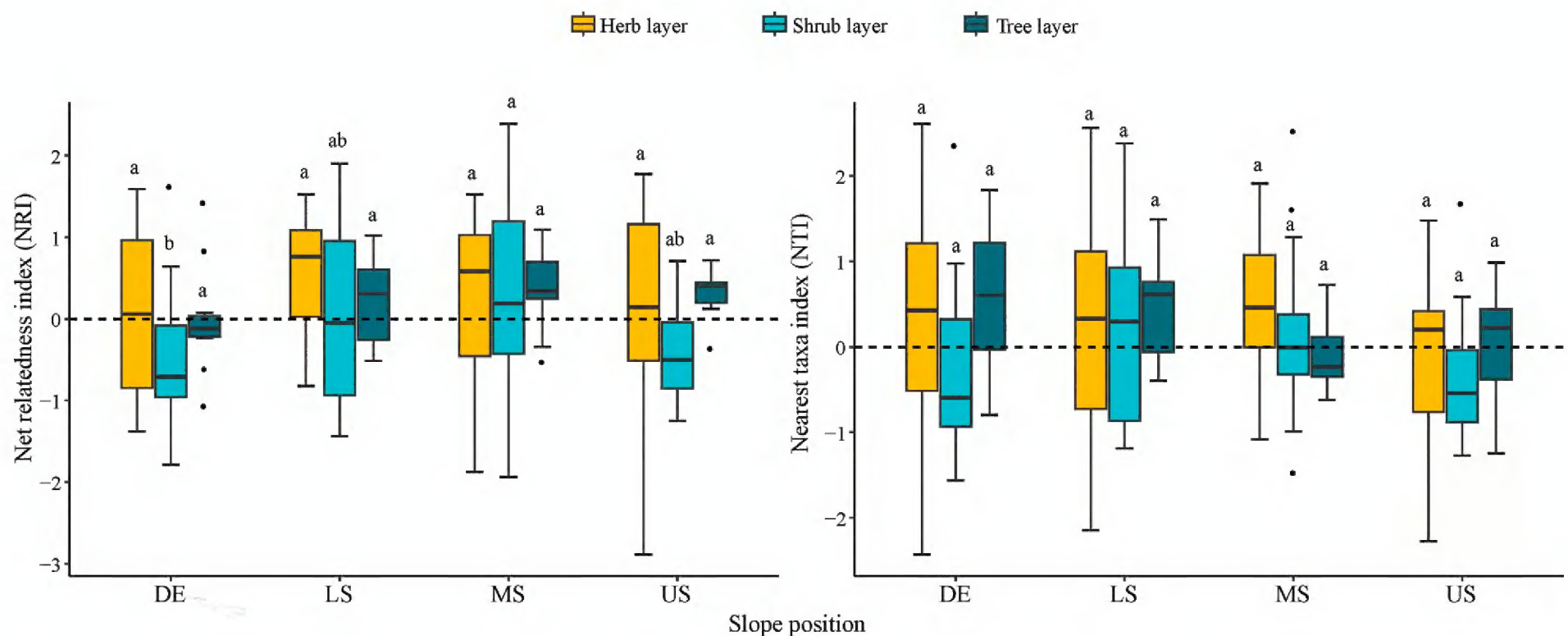
The NRI and NTI in the herb, shrub, and tree layers showed inconsistent patterns in community species phylogenetic relationships across the slope positions (Fig. 4). In the herb layer, both NRI and NTI indicated phylogenetic clustering across the four slope positions. In the shrub layer, both NRI and NTI exhibited phylogenetic divergence on the lower and upper slopes, whereas the middle and depression slopes showed a coexistence of phylogenetic divergence and clustering, with significant differences in NRI among the slope positions ( $p < 0.05$ ). In the tree layer, both NRI and NTI exhibited an overall pattern of phylogenetic clustering on the lower and upper slopes. In contrast, the depression and middle slopes showed a coexistence of phylogenetic divergence and clustering. Overall, the herb and tree layers showed phylogenetic clustering, whereas the shrub layer exhibited phylogenetic divergence.

### Species and phylogenetic diversity in relation to environmental variables

Correlation analysis revealed that species diversity in the herb layer was significantly and negatively correlated with  $\text{NO}_3^-$ -N, SOM, and SWC, and significantly and positively correlated with SP, SA, and SD ( $p < 0.05$ ). The phylogenetic structure was significantly and positively correlated with AK, TP, and BA ( $p < 0.05$ ). Phylogenetic diversity was significantly and negatively correlated with  $\text{NO}_3^-$ -N and SOM contents ( $p < 0.05$ ; Fig. 5).

In the shrub layer, species diversity was significantly and negatively correlated with TP and BA and significantly and positively correlated with SA and pH





**Figure 4.** Changes in phylogenetic structures at different slope positions. Different lowercase letters indicate significant differences between communities at the various slope positions ( $p < 0.05$ ). DE, depression; LS, lower slope; MS, middle slope; US, upper slope.

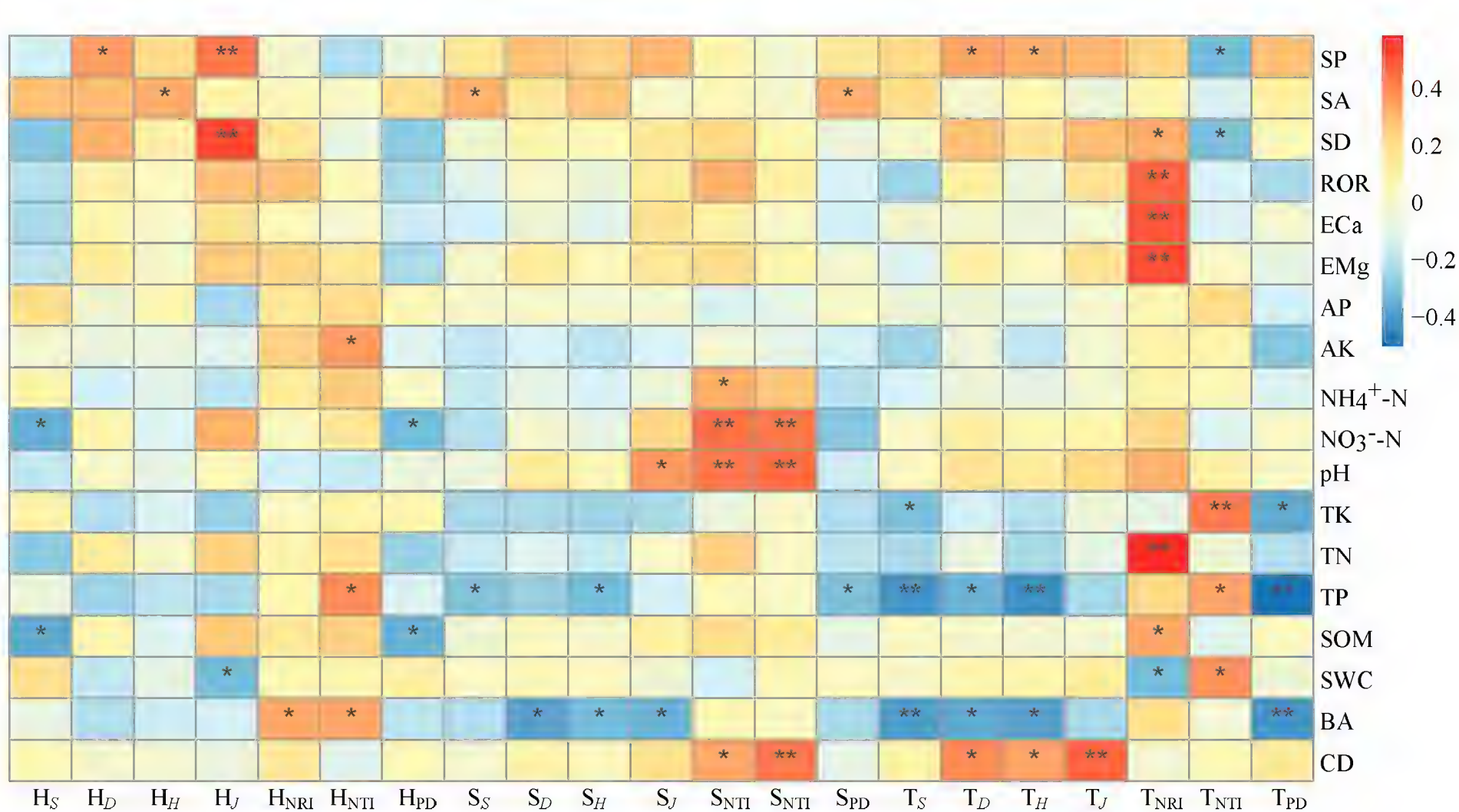
( $p < 0.05$ ). The phylogenetic structure was significantly and positively correlated with  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , pH, and CD ( $p < 0.05$ ). Phylogenetic diversity was significantly and positively correlated with SA and negatively correlated with TP ( $p < 0.05$ ; Fig. 5).

In the tree layer, species diversity was significantly and positively correlated with SP and CD and significantly and negatively correlated with soil TK, TP, and BA ( $p < 0.05$ ). The phylogenetic structure was significantly negatively correlated with SP, SD, and SWC, and significantly positively correlated with SD, ROR, ECa, EMg, TK, TN, TP, SOM, and SWC ( $p < 0.05$ ). Both NRI and NTI showed different responses to SD and SWC. Phylogenetic diversity was significantly negatively correlated with soil TK, TP, and BA ( $p < 0.05$ ; Fig. 5).

In the herb layer, the environmental variables retained in the regression equation collectively explained 24.5%, 13.6%, 19.6%, and 22.1% of the variance in species richness, Simpson index, Shannon–Wiener index, and Pielou index, respectively (Table 1). Among these, SA, SP, and SOM had high explanatory powers for species diversity (Fig. 6). The retained environmental variables in the regression equation collectively explained 14.0% and 16.8% of the variance in NRI and NTI, respectively (Table 1), with BA, ROR, and soil pH contributing significantly (Fig. 6). The environmental factors retained in the regression equation collectively explained 14.6% of the variance in the PD index, with SOM as the main influencing factor (Fig. 6).

In the shrub layer, the environmental variables retained in the regression equation collectively explained 15.1%, 16.9%, 17.0%, and 20.9% of the variance in species richness, Simpson index, Shannon–Wiener index, and Pielou index, respectively (Table 1). Among these, BA, SA, and soil pH had high explanatory powers for species diversity (Fig. 6). The retained environmental variables in the regression equation collectively explained 36.3% and 35.6% of the variance in NRI and NTI, respectively (Table 1), with soil pH,  $\text{NH}_4^+\text{-N}$ , and CD exerting strong influences (Fig. 6). The environmental factors retained in the regression equation collectively explained 21.5% of the variance in the PD index, with SA and soil  $\text{NO}_3^-\text{-N}$  having strong impacts (Fig. 6).





**Figure 5.** Pearson correlation analysis between diversity metrics and environmental factors.  $H_S$ ,  $H_D$ ,  $H_H$ ,  $H_J$ ,  $H_{NRI}$ ,  $H_{NTI}$ , and  $H_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the herb layer, respectively;  $S_S$ ,  $S_D$ ,  $S_H$ ,  $S_J$ ,  $S_{NRI}$ ,  $S_{NTI}$ , and  $S_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the shrub layer, respectively;  $T_S$ ,  $T_D$ ,  $T_H$ ,  $T_J$ ,  $T_{NRI}$ ,  $T_{NTI}$ , and  $T_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the tree layer, respectively. SP, slope position; SA, slope aspect; SD, slope degree; ROR, rock outcrop rate; ECa, exchangeable calcium; EMg, exchangeable magnesium; AP, available phosphorus; AK, available potassium;  $NH_4^+$ -N, ammonium nitrogen;  $NO_3^-$ -N, nitrate nitrogen; pH, soil pH; TK, total potassium; TN, total nitrogen; TP, total phosphorus; SOM, soil organic matter; SWC, soil water content; CD, canopy density; BA, basal area of woody species. \*  $p < 0.05$ ; \*\*  $p < 0.01$ .

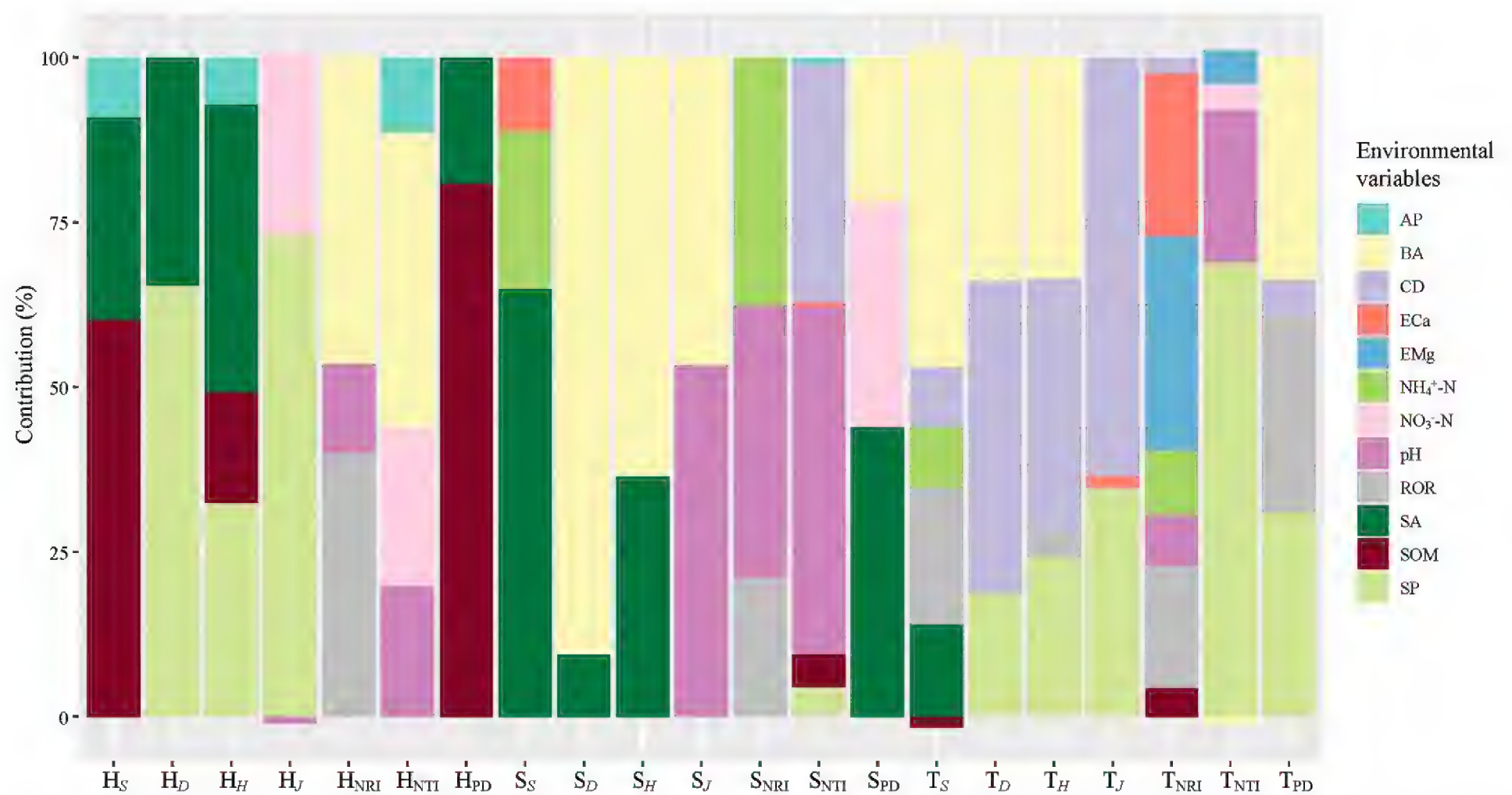
In the tree layer, the environmental variables retained in the regression equation collectively explained 30.1%, 32.7%, 32.1%, and 29.3% of the variance in species richness, Simpson index, Shannon–Wiener index, and Pielou index, respectively (Table 1), with BA, CD, and SP showing the highest explanatory power for species diversity (Fig. 6). The retained environmental variables in the regression equation collectively explained 41.1% and 24.7% of the variance in NRI and NTI, respectively (Table 1). SP, soil EMg, ECa, and pH also had high explanatory powers (Fig. 6). The environmental factors retained in the regression equation collectively explained 32.0% of the variance in the PD index, with SP, ROR, and BA making significant contributions (Fig. 6).

Discussion

Changes in species diversity along karst hillslopes

Plant community distributions result from the combined effects of various environmental factors (climate, soil, topography, and biology) operating at multiple scales. In this study, noticeable differences were observed in topographic, soil, and biological factors along the slope gradient (see Suppl. material 1: table S1), resulting in habitat heterogeneity at different slope positions, which subse-





**Figure 6.** Contribution rates of the environmental variables to the explained variation in species and phylogenetic diversity and structure using hierarchical partitioning analysis.  $H_S$ ,  $H_D$ ,  $H_H$ ,  $H_J$ ,  $H_{NRI}$ ,  $H_{NTI}$ , and  $H_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the herb layer, respectively;  $S_S$ ,  $S_D$ ,  $S_H$ ,  $S_J$ ,  $S_{NRI}$ ,  $S_{NTI}$ , and  $S_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the shrub layer, respectively;  $T_S$ ,  $T_D$ ,  $T_H$ ,  $T_J$ ,  $T_{NRI}$ ,  $T_{NTI}$ , and  $T_{PD}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the tree layer, respectively. SP, slope position; SA, slope aspect; ROR, rock outcrop rate; ECa, exchangeable calcium; EMg, exchangeable magnesium; AP, available phosphorus;  $NH_4^+-N$ , ammonium nitrogen;  $NO_3^- -N$ , nitrate nitrogen; pH, soil pH; SOM, soil organic matter; CD, canopy density; BA, basal area of woody species.

quently affected species diversity in the plant communities. Terrain influences species distribution and diversity by spatially redistributing resources such as soil nutrients, light, heat, and water (Du et al. 2015). Slopes integrate various environmental factors, including light, soil thickness, moisture, and nutrient conditions, which in turn significantly influence plant diversity (Liu et al. 2018). In this study, as slope increased, the species diversity of the herb and shrub layers first decreased and then increased. Species richness in the tree layer showed a similar trend, whereas other diversity indices, such as the Simpson, Shannon–Wiener, and Pielou indices, generally showed a gradual increase (Fig. 2). The elevation of the karst peak-cluster depression is relatively low (<600 m), and there are substantial topographic differences in soil and water availability on the mountainside (Zhang et al. 2021). Conditions in the depression are favorable for plant community species diversity. In contrast, the mountainside contains various microhabitats (rock cliffs, gullies, and open soil) that provide living spaces for plants with different preferences (Zhang et al. 2013). Huang et al. (2016) suggested that conditions on the mountainside may be harsh due to factors such as water scarcity, thin soil, and strong solar radiation, which can make it difficult for any one species to become dominant, thus promoting higher species diversity.

Soil is an essential component of terrestrial ecosystems and is responsible for many ecological processes; therefore, it is a critical factor in research on the renewal and succession of plant communities (Daunoras et al. 2024). In karst



**Table 1.** Stepwise multiple regression equations between species, phylogenetic diversity, structure, and environmental factors.

| Stepwise multiple regression equations                                                                                                                                        | R <sup>2</sup> | P      |
|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|----------------|--------|
| $H_S = 8.426 + 1.598 \text{ SA} + 0.02 \text{ AP} - 0.187 \text{ SOM}$                                                                                                        | 0.245          | 0.004  |
| $H_D = 0.655 + 0.019 \text{ SP} + 0.043 \text{ SA}$                                                                                                                           | 0.136          | 0.025  |
| $H_H = 1.459 + 0.087 \text{ SP} + 0.173 \text{ SA} + 0.004 \text{ AP} - 0.018 \text{ SOM}$                                                                                    | 0.196          | 0.019  |
| $H_J = 1.266 + 0.033 \text{ SP} + 0.004 \text{ NO}_3\text{-N} - 0.073 \text{ pH}$                                                                                             | 0.221          | 0.007  |
| $H_{\text{NRI}} = 4.098 + 0.976 \text{ ROR} - 0.624 \text{ pH} + 0.250 \text{ BA}$                                                                                            | 0.140          | 0.038  |
| $H_{\text{NTI}} = 4.68 + 0.006 \text{ AP} + 0.032 \text{ NO}_3\text{-N} - 0.67 \text{ pH} + 0.238 \text{ BA}$                                                                 | 0.168          | 0.033  |
| $H_{\text{PD}} = 1490.0 + 189.1 \text{ SA} - 27.2 \text{ SOM}$                                                                                                                | 0.146          | 0.020  |
| $S_S = 7.247 + 2.026 \text{ SA} - 0.032 \text{ ECa} - 0.023 \text{ NH}_4\text{+N}$                                                                                            | 0.151          | 0.031  |
| $S_D = 0.695 + 0.071 \text{ SA} - 0.07 \text{ BA}$                                                                                                                            | 0.169          | 0.012  |
| $S_H = 1.412 + 0.308 \text{ SA} - 0.193 \text{ BA}$                                                                                                                           | 0.170          | 0.012  |
| $S_J = -0.001 + 0.119 \text{ pH} - 0.043 \text{ BA}$                                                                                                                          | 0.209          | 0.005  |
| $S_{\text{NRI}} = -9.409 + 1.1924 \text{ ROR} + 0.013 \text{ NH}_4\text{+N} + 1.095 \text{ pH}$                                                                               | 0.363          | <0.001 |
| $S_{\text{NTI}} = -11.97 - 0.269 \text{ SP} - 0.012 \text{ ECa} - 0.01 \text{ AP} + 1.459 \text{ pH} + 0.061 \text{ SOM} + 2.671 \text{ CD}$                                  | 0.356          | 0.002  |
| $S_{\text{PD}} = 667.73 + 182.39 \text{ SA} - 9.05 \text{ NO}_3\text{-N} - 76.44 \text{ BA}$                                                                                  | 0.215          | 0.008  |
| $T_S = 9.542 + 5.798 \text{ SA} - 14.392 \text{ ROR} - 0.092 \text{ NH}_4\text{+N} + 0.444 \text{ SOM} - 4.216 \text{ BA} + 30.01 \text{ CD}$                                 | 0.301          | 0.006  |
| $T_D = 0.426 + 0.021 \text{ SP} - 0.055 \text{ BA} + 0.531 \text{ CD}$                                                                                                        | 0.327          | 0.001  |
| $T_H = 0.882 + 0.162 \text{ SP} - 0.641 \text{ ROR} - 0.185 \text{ BA} + 2.142 \text{ CD}$                                                                                    | 0.321          | 0.001  |
| $T_J = 0.3344 + 0.0517 \text{ SP} - 0.002 \text{ ECa} + 0.001 \text{ AP} + 0.479 \text{ CD}$                                                                                  | 0.293          | 0.003  |
| $T_{\text{NRI}} = -2.985 + 0.588 \text{ ROR} + 0.012 \text{ ECa} + 0.108 \text{ EMg} + 0.007 \text{ NH}_4\text{+N} + 0.423 \text{ pH} - 0.034 \text{ SOM} - 1.751 \text{ CD}$ | 0.411          | 0.001  |
| $T_{\text{NTI}} = -8.140 - 0.441 \text{ SP} + 0.131 \text{ EMg} - 0.032 \text{ NO}_3\text{-N} + 1.249 \text{ pH} - 0.257 \text{ BA}$                                          | 0.247          | 0.011  |
| $T_{\text{PD}} = 1376.9 + 248.4 \text{ SP} - 1324.3 \text{ ROR} - 159.7 \text{ BA} + 1444.5 \text{ CD}$                                                                       | 0.320          | 0.001  |

$H_S$ ,  $H_D$ ,  $H_H$ ,  $H_J$ ,  $H_{\text{NRI}}$ ,  $H_{\text{NTI}}$ , and  $H_{\text{PD}}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the herb layer, respectively;  $S_S$ ,  $S_D$ ,  $S_H$ ,  $S_J$ ,  $S_{\text{NRI}}$ ,  $S_{\text{NTI}}$ , and  $S_{\text{PD}}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the shrub layer, respectively;  $T_S$ ,  $T_D$ ,  $T_H$ ,  $T_J$ ,  $T_{\text{NRI}}$ ,  $T_{\text{NTI}}$ , and  $T_{\text{PD}}$  indicate the species richness, Simpson index, Shannon–Wiener index, Pielou index, net relatedness index, nearest taxon index, and phylogenetic diversity of the tree layer, respectively. SP, slope position; SA, slope aspect; SD, slope degree; ROR, rock outcrop rate; ECa, exchangeable calcium; EMg, exchangeable magnesium; AP, available phosphorus; AK, available potassium;  $\text{NH}_4\text{+N}$ , ammonium nitrogen;  $\text{NO}_3\text{-N}$ , nitrate nitrogen; pH, soil pH; TK, total potassium; TN, total nitrogen; TP, total phosphorus; SOM, soil organic matter; SWC, soil water content; CD, canopy density; BA, basal area of woody species.

areas, plant roots are widely distributed in surface soil, the quality of which determines its favorability for plant growth (Yan et al. 2022). Numerous studies have demonstrated that the physicochemical properties of soil have a significant impact on plant diversity (Sheng et al. 2015; Guo et al. 2018; Gastauer et al. 2020). In this study, the diversity of the herb, shrub, and tree layers was influenced by multiple soil factors. The species diversity of the herb layer was significantly negatively correlated with soil  $\text{NO}_3\text{-N}$ , SOM, and SWC. However, in the shrub layer, it was negatively correlated with soil TP but positively correlated with pH. In contrast, diversity in the tree layer was negatively correlated with soil TK and TP. Although nitrogen and phosphorus are widely recognized as the primary limiting nutrients for terrestrial plants globally (Borer et al. 2015), our study site in the tropical karst region aligns with findings identifying phosphorus and potassium as key limiting elements (Tan et al. 2019). This difference highlights the uniqueness of the karst ecosystem and suggests that potassium limitation may replace nitrogen as a key constraint alongside phosphorus in this environment. Borer et al. (2015) detected widespread phosphorus limitation at the tree species level in tropical forests, suggesting that intense competition for soil phosphorus may be a common phenomenon at the species scale. Han et al. (2021) indicated that



soil potassium is a major nutrient-limiting factor in the subtropical karst areas of Guangxi, China. Our study provides further evidence that soil phosphorus and potassium are key factors limiting plant species diversity in karst areas.

Plants interact with their local environment, leading to changes in community species composition and distribution, which, in turn, affect community species diversity (Gaiarsa et al. 2025). In this study, species diversity in the shrub and tree layers was significantly negatively correlated with BA, whereas CD primarily affected species diversity in the tree layer. You et al. (2016) found that basal area was the most significant factor influencing the composition of shrub layer species in the community. An increased basal area, reflecting a higher presence of large-diameter trees, suppresses the growth of small-diameter plants, leading to negative interactions at a small scale. As the forest naturally thins, community species diversity decreases accordingly (Chen et al. 2023). Canopy closure is a key factor in studying understory plant diversity (Jules et al. 2008; You et al. 2016) because it limits light availability, thereby mitigating plant competition for resources within the community. Consequently, competition has a less significant impact on the tree layer, resulting in reduced interspecific competition, which increases the diversity of tree layer species (Jules et al. 2008; Chen et al. 2023). This study reveals that biological, topographic, and edaphic factors have important effects on the distribution patterns of community species diversity across three forest strata (herb, shrub, and tree layers) in the TKSR. The divergent responses of these plant layers to both biotic and abiotic environmental factors result in measurable variations in species diversity along slope gradients. Nevertheless, the coupled effects of these factors on the pattern of community species diversity require further exploration.

### Changes in phylogenetic diversity along karst hillslopes

High phylogenetic diversity suggests that spatial habitats can support the coexistence of species with relatively high levels of evolutionary diversity and variation, as well as longer evolutionary histories (Zeng et al. 2018). In this study, the phylogenetic diversity of the herb, shrub, and tree layers initially decreased and then increased with increasing slope position, exhibiting significant differences in phylogenetic diversity across the slope gradient in the herb layer. Plant communities in the depressions and upper slopes exhibited higher species diversity, corresponding to longer evolutionary histories and higher levels of evolutionary diversity and variation. Conversely, plant communities on the lower and middle slopes showed opposite trends. Xiao et al. (2019) suggested that the different phylogenetic diversity responses of species with different life forms to slope variation are related to their adaptive strategies to different environments. The species richness of woody plant communities is primarily determined by climatic factors such as low winter temperatures (Watanabe et al. 2024), whereas microenvironmental factors such as light intensity, soil moisture, and nutrient status in the understory are the main determinants of herbaceous plant community composition (Reich et al. 2012). This may explain why the phylogenetic diversity of the herb layer changed significantly with an increase in slope position in the peak-cluster depression. In contrast, the phylogenetic diversity of the shrub and tree layers did not show a significant trend. In this study, SA and SOM both had significant effects on the phylogenetic diversity of the herb layer; SA,  $\text{NO}_3\text{-N}$ , and BA significantly affected the phylogenetic diversity of the shrub layer; and SP, ROR, BA, and CD significantly



influenced the phylogenetic diversity of the tree layer. Generally, sunny slopes with favorable light conditions promote plant growth, whereas relatively low levels of soil moisture on shaded slopes can inhibit plant growth. Thus, slope aspect may either promote or restrict community species richness (Liu et al. 2018; Zhang et al. 2020). In this study, communities on sunny slopes had greater species richness and higher phylogenetic diversity than those on shaded slopes in the herb and shrub layers, possibly due to the relatively favorable habitat conditions on sunny slopes, which enabled plants to reproduce more rapidly. Species continuously evolve and diversify to occupy suitable ecological niches, thereby increasing the phylogenetic diversity of their communities. Previous studies have indicated that species with different life forms respond differently to the same habitat conditions (Ding et al. 2015), and similar results were obtained in this study. Phylogenetic diversity research can help determine which communities should be prioritized for conservation within a region, as communities with higher phylogenetic diversity have greater evolutionary potential and a stronger ability to cope with risks associated with global change (Devictor et al. 2010). The results indicate that communities in depressions and on upper slopes have higher conservation value because of their greater species and phylogenetic diversity.

### Changes in phylogenetic structure along karst hillslopes

Community phylogenetic structures result from the interactions among ecological factors, environmental filtering, and historical evolution, and they can reveal the primary ecological processes influencing species diversity (Zhang et al. 2016). Based on the assumption of phylogenetic niche conservatism, environmental filtering leads to the coexistence of species with similar physiological tolerances, resulting in an aggregated relationship among phylogenetic lineages within the community. Interspecific competition enables distantly related species to coexist within a community, resulting in divergent relationships among phylogenetic lineages (Webb et al. 2002). In this study, the overall phylogenetic structures of the herb and tree layer communities tended to be aggregated, whereas that of the shrub layer community tended to be divergent. This suggests that the herb and tree layer communities were primarily composed of closely related species and that environmental filtering was the main ecological process influencing community assembly. In contrast, the species in the shrub layer community were more distantly related, and the primary ecological process influencing their community assembly was competitive exclusion. This may be associated with spatial scale, as interspecific competition often occurs when resources within a habitat are limited. In this study, the relatively small sampling area of the shrub layer may have exacerbated competition among species owing to restricted space and resources, leading to the coexistence of different species occupying different niches (Zhu et al. 2018). On a larger scale, environmental filtering leads to the coexistence of species with similar resource utilization, resulting in a more aggregated phylogenetic structure within the community. Studies have shown that closely related species are unlikely to coexist at small scales, leading to significant phylogenetic divergence within the community (Silva and Batalha 2009). As spatial scale increases, phylogenetic structures in communities gradually shift from divergent to aggregated (Jin et al. 2020), a trend that is particularly evident in tropical rainforests (Hubbell 2006). Furthermore, strong environmental filtering in karst habitats results in various phylogenetic



structural patterns within plant communities, which are influenced by multiple environmental factors at different levels. Specifically, phylogenetic aggregation in the herb layer was associated with increases in soil AK, TP, and BA. In the shrub layer, aggregation was driven by elevated soil  $\text{NH}_4^+\text{-N}$ ,  $\text{NO}_3^-\text{-N}$ , pH, and BA. Conversely, the tree layer responded to increases in soil ECa, EMg, TK, TN, TP, SOM, and ROR. However, an increase in SD promoted an overall aggregation trend in the phylogenetic relationships of tree layer species, whereas SOM had the opposite effect, increasing the phylogenetic distance between adjacent species and affecting the phylogenetic structure of the tree layer. The phylogenetic structure of plant communities is closely related to the response of plants to their environment, which in turn affects the ecological processes that dominate community assembly.

The phylogenetic structures of the herb, shrub, and tree layers exhibited inconsistent patterns along the slope gradient. The herb layers across the different slopes exhibited aggregated phylogenetic structures. In addition to the influence of microhabitat conditions, the phylogenetic structure of the herb layer may be related to the life histories of herbaceous plants (Qian et al. 2014). Herbaceous plants have short life cycles and strong dispersal abilities, can rapidly occupy suitable habitats, exhibit large population fluctuations, and easily form aggregated phylogenetic structures (Niu et al. 2011). The dispersal of tree seeds may also influence the phylogenetic structure of the herb layer community. Herb layers include woody plant seedlings, and the limited dispersal of seeds from parent trees in the forest leads to a clustered pattern of seedlings, resulting in an aggregated phylogenetic structure in the herb layer community (Niu et al. 2011). The phylogenetic structure of the shrub layer exhibited divergence in the depression and upper slope and aggregation in the middle slope communities. In contrast, the lower slope communities showed inconsistent NRI and NTI values for the phylogenetic relationships of community species, with NRI indicating divergence and NTI indicating aggregation. In the tree-layer communities, the NRI and NTI of the depression and middle slopes exhibited inconsistent phylogenetic structures. In the depression, NRI showed divergence, whereas NTI showed aggregation. Conversely, the opposite pattern was observed in the middle slope communities, while the phylogenetic structures of the upper and lower slope communities were aggregated. In high-altitude areas, due to environmental stress, species within communities undergo convergent evolution, resulting in a trend toward aggregated phylogenetic structures (Kluge and Kessler 2011; You et al. 2013). Similarly, research has shown that the phylogenetic structures of evergreen broad-leaved forest communities exhibit aggregation in low-altitude areas and divergence in high-altitude areas (Huang et al. 2010). In this study, the harsh habitat conditions on the upper slope may have caused strong environmental stress, promoting convergent evolution in plants and resulting in aggregated phylogenetic structures in the tree-layer communities. Conversely, competition for limited resources among plants may have caused the phylogenetic structure of shrub layer plants to diverge. The inconsistent changes in community NRI and NTI values are related to their different emphases, indicating that distinct ecological processes influence the assembly of herb, shrub, and tree layer communities. The different ways in which communities respond to the environment affect the relative importance of ecological processes in community assembly. The results indicate that deterministic processes (environmental filtering and competitive exclusion) have significant impacts on com-



munity assembly in the TKSR, while some communities may also be influenced by neutral processes ( $\text{NRI}$  or  $\text{NTI} < -1.96$ ) (Vamosi et al. 2009).

### Conservation of karst forests

Karst landscapes are crucial biodiversity reservoirs, particularly in Asia, hosting a wealth of endemic species (Clements et al. 2006). The steep karst regions of southwestern China are recognized as biodiversity hotspots, notable for their remarkable plant species richness and significant conservation value (Guo et al. 2018; Geekiyanage et al. 2019). Protecting biodiversity and rehabilitating degraded vegetation in these areas remain pivotal ecological priorities for the Chinese government and researchers (Chen et al. 2024). Conservation strategies should incorporate phylogenetic diversity into assessment frameworks, complementing traditional species diversity metrics to reflect evolutionary relationships (Tietje et al. 2023). Consequently, areas with high and unique phylogenetic diversity should be prioritized for conservation efforts (Zhang et al. 2024). Our study demonstrates that depressions and upper slopes exhibit greater species and phylogenetic diversity than other slope positions, highlighting their significant conservation value for plant diversity. Karst depressions, characterized by deep, fertile soils, are especially susceptible to anthropogenic conversion. In southwestern China, this has resulted in substantial natural forest loss and degradation, primarily due to their conversion into agricultural and plantation lands (Yuan et al. 2024). Therefore, conservation efforts for forests in karst depressions should be prioritized. Our findings provide critical insights for planning forest reserves and developing conservation strategies in karst regions.

### Conclusion

The results show that species diversity in the herb and shrub layers initially decreases and then increases. In contrast, species richness in the tree layer initially increases and then decreases, while the remaining indices show an overall increasing trend in the TKSR along steep karst hillslopes. Stepwise regression analysis revealed that SA, SP, and SOM all have high explanatory power for species diversity in the herb layer. BA, SA, and soil pH explained much of the variation in species diversity in the shrub layer, whereas BA, CD, and SP had strong influences on species diversity in the tree layer. Phylogenetic diversity in the herb, shrub, and tree layers initially decreased and then increased as the slope gradient increased. Plant communities exhibited relatively high phylogenetic diversity in the depressions and on the upper slopes, suggesting longer evolutionary histories and greater evolutionary diversity and variation. In contrast, plant communities on the lower and middle slopes had relatively lower phylogenetic diversity. SA and SOM collectively had significant effects on the phylogenetic diversity of the herb layer; SA,  $\text{NO}_3^-$ -N, and BA significantly influenced the phylogenetic diversity of the shrub layer; and SP, ROR, BA, and CD had significant effects on the phylogenetic diversity of the tree layer. The herb and tree layers exhibited phylogenetic clustering, and habitat filtering was the primary ecological process influencing community assembly. The shrub layer exhibited phylogenetic overdispersion, and competitive exclusion was the primary ecological process influencing community assembly. BA, ROR, and soil pH were the primary factors influencing



the phylogenetic structure of the herb layer; soil pH,  $\text{NH}_4^+\text{-N}$ , and CD strongly influenced the phylogenetic structure of the shrub layer; and soil EMg, ECa, pH, and SP had high explanatory power for the phylogenetic structure of the tree layer. Overall, the results show that deterministic processes (habitat filtering and competitive exclusion) have significant impacts on community assembly in the TKSR; however, some communities are also influenced by neutral processes. Furthermore, depressions and upper slopes have higher conservation value because of their higher levels of species and phylogenetic diversity in southwestern China.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Use of AI

No use of AI was reported.

### Funding

This work was supported by the Guangxi Natural Science Foundation (2021GXNSF-FA196005, 2021GXNSFAA196024, 2022GXNSFBA035633, 2022GXNSFBA035461); the Special Funding for Guangxi Bagui Young Top Talents Program (to Zhonghua Zhang); and the National Natural Science Foundation of China (31960275, 31760128).

### Author contributions

Qingling Pang: Conceptualization; data curation; methodology; writing—original draft. Cong Hu: Funding acquisition; supervision; writing—original draft. Chaohao Xu: supervision; writing—original draft. Chaofang Zhong: supervision; writing—original draft. Zhonghua Zhang: Conceptualization; funding acquisition; supervision; visualization; writing—review and editing. Gang Hu: Project administration; supervision; visualization; writing—review and editing.

### Author ORCIDs

Qingling Pang  <https://orcid.org/0009-0002-1168-7402>

Cong Hu  <https://orcid.org/0000-0001-7507-4520>

Chaohao Xu  <https://orcid.org/0000-0002-0437-5390>

Chaofang Zhong  <https://orcid.org/0000-0002-3509-3628>

Zhonghua Zhang  <https://orcid.org/0000-0003-2094-698X>

Gang Hu  <https://orcid.org/0000-0002-0662-811X>

### Data availability

All data that support the findings of this study are available upon request.

## References

Bagaria G, Rodà F, Pino J (2019) Extinction and colonisation of habitat specialists drive plant species replacement along a Mediterranean grassland-forest succession. *Journal of Vegetation Science* 30: 331–340. <https://doi.org/10.1111/jvs.12722>



- Bao S (2000) Soil and Agricultural Chemistry Analysis. China Agriculture Press, Beijing.
- Berry ZC, Gotsch SG, Holwerda F, Muñoz-Villers LE, Asbjornsen H (2016) Slope position influences vegetation-atmosphere interactions in a tropical montane cloud forest. *Agricultural and Forest Meteorology* 221: 207–218. <https://doi.org/10.1016/j.agrformet.2016.02.012>
- Borer ET, Lind EM, Ogdahl EJ, Seabloom EW, Tilman D, Montgomery RA, Kinkel LL (2015) Food-web composition and plant diversity control foliar nutrient content and stoichiometry. *Journal of Ecology* 103: 1432–1441. <https://doi.org/10.1111/1365-2745.12461>
- Chen B, Jiang L, Xie ZY, Li YD, Li JX, Li MJ, Wei CS, Xing C, Liu JF, He ZS (2021) Taxonomic and phylogenetic diversity of plants in a *Castanopsis kawakami* natural forest. *Biodiversity Science* 29: 439–448. <https://doi.org/10.17520/biods.2020399>
- Chen C, Zhang SJ, Li LD, Liu ZD, Chen JL, Gu X, Wang LF, Fang X (2019) Carbon, nitrogen and phosphorus stoichiometry in leaf, litter and soil at different vegetation restoration stages in the mid-subtropical region of China. *Acta Phytocologica Sinica* 43: 658–671. <https://doi.org/10.17521/cjpe.2019.0018>
- Chen S, Wang CL, Ren YC, Zhang HF, Zhou DD, Li J, Song HJ, Yang XQ (2023) Spatial autocorrelation patterns and influencing factors of tree radial growth in the secondary *Picea* forest in Guandi Mountains, northern China. *Acta Ecologica Sinica* 43: 1572–1583. <https://doi.org/10.5846/stxb202203080550>
- Chen Y, Cheng C, Xiong K, Rong L, Zhang S (2024) Quantifying the biodiversity and ecosystem service outcomes of karst ecological restoration: A meta-analysis of South China Karst. *Catena* 245: 108278. <https://doi.org/10.1016/j.catena.2024.108278>
- Ci XQ, Li J (2017) Phylogenetic diversity and its application in floristics and biodiversity conservation. *Biodiversity Science* 25: 175–181. <https://doi.org/10.17520/biods.2016183>
- Clements R, Sodhi NS, Schilthuizen M, Ng PKL (2006) Limestone karsts of Southeast Asia: Imperiled arks of biodiversity. *Bioscience* 56: 733–742. [https://doi.org/10.1641/0006-3568\(2006\)56\[733:LKOSA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[733:LKOSA]2.0.CO;2)
- Daunoras J, Kačergius A, Gudiukaitė R (2024) Role of soil microbiota enzymes in soil health and activity changes depending on climate change and the type of soil ecosystem. *Biology (Basel)* 13(2): 85. <https://doi.org/10.3390/biology13020085>
- De Waele J (2017) Karst processes and landforms. *The International Encyclopedia of Geography*. John Wiley and Sons, New York. <https://doi.org/10.1002/9781118786352.wbieg0968>
- Deák B, Kovács B, Rádai Z, Apostolova I, Kelemen A, Kiss R, Lukács K, Palpurina S, Sopotlieva D, Báthori F, Valkó O (2021) Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes. *The Science of the Total Environment* 763: 144199. <https://doi.org/10.1016/j.scitotenv.2020.144199>
- Devictor V, Mouillot D, Meynard C, Jiguet F, Thuiller W, Mouquet N (2010) Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters* 13: 1030–1040. <https://doi.org/10.1111/j.1461-0248.2010.01493.x>
- Ding HB, Wu ZL, Lv DP, Wu QJ, Shan MY, Bai HT, Luo K (2015) Community phylogenetic structural characteristics of various secondary forests in mountainous eastern Yunnan. *Shengtaixue Zazhi* 34: 2720–2726.
- Dong LB, Li JW, Zhang Y, Bing MY, Liu YL, Wu JZ, Hai XY, Li A, Wang KB, Wu PX, Shanguan ZP, Deng L (2022) Effects of vegetation restoration types on soil nutrients and soil erodibility regulated by slope positions on the Loess Plateau. *Journal of Environmental Management* 302: 113985. <https://doi.org/10.1016/j.jenvman.2021.113985>



- Du H, Peng WX, Song TQ, Zeng FP, Wang KL, Song M, Zhang H (2015) Spatial pattern of woody plants and their environmental interpretation in the karst forest of southwest China. *Plant Biosystems* 149: 121–130. <https://doi.org/10.1080/11263504.2013.796019>
- Faith DP (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation* 61: 1–10. [https://doi.org/10.1016/0006-3207\(92\)91201-3](https://doi.org/10.1016/0006-3207(92)91201-3)
- Gaiarsa MP, Mora BB, Kremen C, Ponisio LC (2025) Changes in species composition and community structure during plant–pollinator community assembly. *Ecology* 106(6): e70119. <https://doi.org/10.1002/ecy.70119>
- Gastauer M, Thiele J, Porembski S, Neri AV (2020) How do altitude and soil properties influence the taxonomic and phylogenetic structure and diversity of Brazilian páramo vegetation? *Journal of Mountain Science* 17: 1045–1057. <https://doi.org/10.1016/j.biocon.2015.01.031>
- Geekiyanage N, Goodale UM, Cao K, Kitajima K (2019) Plant ecology of tropical and subtropical karst ecosystems. *Biotropica* 51: 626–640. <https://doi.org/10.1111/btp.12696>
- Geng QW, Muhammad A, Yuan ZX, Zheng J, He XR, Ding DD, Yin F, Li CX (2022) Plant species composition and diversity along successional gradients in arid and semi-arid regions of China. *Forest Ecology and Management* 524: 120542. <https://doi.org/10.1016/j.foreco.2022.120542>
- Gong X, Brueck H, Giese KM, Zhang L, Sattelmacher B, Lin S (2008) Slope aspect has effects on productivity and species composition of hilly grassland in the Xilin River Basin, Inner Mongolia, China. *Journal of Arid Environments* 72: 483–493. <https://doi.org/10.1016/j.jaridenv.2007.07.001>
- Guo YL, Wang B, Mallik AU, Huang FZ, Xiang WS, Ding T, Wen SJ, Lu SH, Li DX, He LY, Li XK (2017) Topographic species–habitat associations of tree species in a heterogeneous tropical karst seasonal rain forest, China. *Journal of Plant Ecology* 10: 450–460. <https://doi.org/10.1093/jpe/rtw057>
- Guo YL, Xiang WS, Wang B, Li DX, Mallik AU, Chen HYH, Huang FZ, Ding T, Wen SJ, Lu SH, Li XK (2018) Partitioning beta diversity in a tropical karst seasonal rainforest in Southern China. *Scientific Reports* 8: 17408. <https://doi.org/10.1038/s41598-018-35410-7>
- Han TF, Huang J, Liu KL, Fan HZ, Shi XJ, Chen J, Jiang XJ, Liu GR, Liu SJ, Zhang L, Xu YM, Feng G, Zhang HM (2021) Soil potassium regulation by changes in potassium balance and iron and aluminum oxides in paddy soils subjected to long-term fertilization regimes. *Soil & Tillage Research* 214: 105168. <https://doi.org/10.1016/j.still.2021.105168>
- Hu QJ, Sheng MY, Bai YX, Jie Y, Xiao HL (2020) Response of C, N, and P stoichiometry characteristics of *Broussonetia papyrifera* to altitude gradients and soil nutrients in the karst rocky ecosystem, SW China. *Plant and Soil* 475: 1–14. <https://doi.org/10.1007/s11104-020-04742-7>
- Huang FZ, Ding T, Li XK, Guo YL, Wang B, Xiang WS, Wen SJ, Li DX, He YL (2016) Species diversity for various associations along an altitudinal gradient in the karst seasonal rainforest in Nonggang. *Acta Ecologica Sinica* 36: 4509–4517. <https://doi.org/10.5846/stxb201411232324>
- Huang JX, Zheng FY, Mi XC (2010) Influence of environmental factors on phylogenetic structure at multiple spatial scales in an evergreen broad-leaved forest of China. *Acta Phytocologica Sinica* 34: 309–315. <https://doi.org/10.3773/j.issn.1005-264x.2010.03.008>
- Huang YS, Wu WH, Jiang RH, Liu SY, Liu Y, Li XK (2013) Primary study on species diversity of plant in Nonggang. *Guihaia* 33: 346–355, 345.



- Hubbell SP (2006) Neutral theory and the evolution of ecological equivalence. *Ecology* 87: 1387–1398. [https://doi.org/10.1890/0012-9658\(2006\)87\[1387:ntateo\]2.0.co;2](https://doi.org/10.1890/0012-9658(2006)87[1387:ntateo]2.0.co;2)
- Jiang ZC, Lian YQ, Qin XQ (2014) Rocky desertification in Southwest China: Impacts, causes, and restoration. *Earth-Science Reviews* 132: 1–12. <https://doi.org/10.1016/j.earscirev.2014.01.005>
- Jin LS, Yin DY, Fortin MJ, Cadotte MW (2020) The mechanisms generating community phylogenetic patterns change with spatial scale. *Oecologia* 193(3): 655–664. <https://doi.org/10.1007/s00442-020-04695-9>
- Jin Y, Qian HV (2019) PhyloMaker: An R package that can generate very large phylogenies for vascular plants. *Ecography* 42: 1353–1359. <https://doi.org/10.1111/ecog.04434>
- Jules MJ, Sawyer JO, Jules ES (2008) Assessing the relationships between stand development and understory vegetation using a 420-year chronosequence. *Forest Ecology and Management* 255: 2384–2393. <https://doi.org/10.1016/j.foreco.2007.12.042>
- Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO (2008) Picante: Tools for integrating phylogenies and ecology. *Bioinformatics* (Oxford, England) 26: 1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kembel SW, Hubbell SP (2006) The phylogenetic structure of a neotropical forest tree community. *Ecology* 87: S86–S99. [https://doi.org/10.1890/0012-9658\(2006\)87\[86:T-PSOAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[86:T-PSOAN]2.0.CO;2)
- Kluge J, Kessler M (2011) Phylogenetic diversity, trait diversity and niches: Species assembly of ferns along a tropical elevational gradient. *Journal of Biogeography* 38: 394–405. <https://doi.org/10.1111/j.1365-2699.2010.02433.x>
- Lai JS, Zou Y, Zhang JL, Peres-Neto PR (2022) Generalizing hierarchical and variation partitioning in multiple regression and canonical analyses using the rdacca. hp R package. *Methods in Ecology and Evolution* 13: 782–788. <https://doi.org/10.1111/2041-210x.13800>
- Li ZR, Colinet G, Zu YQ, Wang JX, An LZ, Li Q, Niu XY (2019) Species diversity of *Arabis alpina* L. communities in two Pb/Zn mining areas with different smelting history in Yunnan Province, China. *Chemosphere* 233: 603–614. <https://doi.org/10.1016/j.chemosphere.2019.05.228>
- Liang T, Tian F, Zou L, Jin H, Tagesson T, Rumpf S, He T, Liang S, Fensholt R (2024) Global assessment of vegetation patterns along topographic gradients. *International Journal of Digital Earth* 17: 2404232. <https://doi.org/10.1080/17538947.2024.2404232>
- Liu B (2017) Vertical patterns in plant diversity and their relations with environmental factors on the southern slope of the Tianshan Mountains (middle section) in Xinjiang (China). *Journal of Mountain Science* 14: 742–757. <https://doi.org/10.1007/s11629-016-4110-4>
- Liu GC, Huang YX, Wang QG, Xing YJ (2018) Effects of environmental factors on plant species diversity: Research progress. *Zhongguo Nongxue Tongbao* 34: 83–89.
- Lu M, Zhao JX, Lu ZR, Li MJ, Yang JF, Fullen M, Li YM, Fan MP (2023) Maize–soybean intercropping increases soil nutrient availability and aggregate stability. *Plant and Soil* 6: 1–16. <https://doi.org/10.1007/s11104-023-06282-2>
- Lu RK (1999) *Analysis Methods of Soil Agricultural Chemistry*. Beijing: China Agricultural Science and Technology Press.
- Ma RX, Guo YL, Li DX, Wang B, Xiang WS, Huang FZ, Lu F, Wen SJ, Li JX, Lu SH, Li XK (2023) Spatial distribution pattern and mechanism of sapling regeneration in karst seasonal rainforest in southwestern Guangxi. *Biodiversity Science* 31: 17–26. <https://doi.org/10.17520/biods.2022251>



- MacDonald ZG, Nielsen SE, Acorn JH (2017) Negative relationships between species richness and evenness render common diversity indices inadequate for assessing long-term trends in butterfly diversity. *Biodiversity and Conservation* 26: 617–629. <https://doi.org/10.1007/s10531-016-1261-0>
- Meng Q, Wang S, Fu Z, Deng Y, Chen H (2022) Soil types determine vegetation communities along a toposequence in a dolomite peak-cluster depression catchment. *Plant and Soil* 475: 5–22. <https://doi.org/10.1007/s11104-022-05308-5>
- Myers JA, Chase JM, Jiménez I, Jørgensen PM, Araujo-Murakami A, Paniagua-Zambrana N, Seidel R (2013) Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology Letters* 16: 151–157. <https://doi.org/10.1111/ele.12021>
- Nettesheim FC, Garbin ML, Rajao PH, Araujo DS, Grelle CE (2018) Environment is more relevant than spatial structure as a driver of regional variation in tropical tree community richness and composition. *Plant Ecology & Diversity* 11: 27–40. <https://doi.org/10.1080/17550874.2018.1473520>
- Niu HY, Wang ZF, Lian JY, Ye WH, Shen H (2011) New progress in community assembly: Community phylogenetic structure combining evolution and ecology. *Biodiversity Science* 19: 275–283. <https://doi.org/10.3724/sp.j.1003.2011.09275>
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2019) Package 'Vegan'—Community Ecology Package. <https://cran.r-project.org/web/packages/vegan/index.html>
- Peng W, Zhu Y, Song M, Du H, Song T, Zeng F, Zhang F, Wang K, Luo Y, Lan X, Zhang J (2019) The spatial distribution and drivers of soil microbial richness and diversity in a karst broadleaf forest. *Forest Ecology and Management* 449: 117241. <https://doi.org/10.1016/j.foreco.2019.03.033>
- Qian H, Hao ZQ, Zhang J (2014) Phylogenetic structure and phylogenetic diversity of angiosperm assemblages in forests along an elevational gradient in Changbaishan, China. *Journal of Plant Ecology* 7: 154–165. <https://doi.org/10.1093/jpe/rtt072>
- Qiu Y, Zhang JT (2000) The ordination axes clustering based on detrended canonical correspondence analysis ordination and its application to the analysis of the ecological gradients of plant communities. *Acta Ecologica Sinica* 2: 199–206.
- Ramírez-Bautista A, Williams JN (2018) The importance of productivity and seasonality for structuring small rodent diversity across a tropical elevation gradient. *Oecologia* 190: 275–286. <https://doi.org/10.1007/s00442-018-4287-z>
- Reich PB, Frelich LE, Voldseth RA, Bakken P, Adair EC (2012) Understorey diversity in southern boreal forests is regulated by productivity and its indirect impacts on resource availability and heterogeneity. *Journal of Ecology* 100: 539–545. <https://doi.org/10.1111/j.1365-2745.2011.01922.x>
- Santillán V, Quitián M, Tinoco BA, Zárate E, Schleuning M, Böhning-Gaese K, Neuschulz EL (2020) Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain. *Acta Oecologica* 102: 103500. <https://doi.org/10.1016/j.actao.2019.103500>
- Sharma N, Kala CP (2022) Patterns in plant species diversity along the altitudinal gradient in Dhauladhar mountain range of the North-West Himalaya in India. *Trees, Forests and People* 7: 100196. <https://doi.org/10.1016/j.tfp.2022.100196>
- Sheng MY, Xiong KN, Cui GY, Liu Y (2015) Plant diversity and soil physical-chemical properties in karst rocky desertification ecosystem of Guizhou, China. *Acta Ecologica Sinica* 35: 434–448. <https://doi.org/10.5846/stxb201303220488>



- Silva IA, Batalha MA (2009) Phylogenetic overdispersion of plant species in southern Brazilian savannas. *Brazilian Journal of Biology* 69: 843–849. <https://doi.org/10.1590/s1519-69842009000400011>
- Smith SA, Brown JW (2018) Constructing a broadly inclusive seed plant phylogeny. *American Journal of Botany* 105: 302–314. <https://doi.org/10.1002/ajb2.1019>
- Sun J, Wen ZX, Feijó A, Cheng JL, Wang YQ, Li S, Ge DY, Xia L, Yang QS (2020) Elevation patterns and critical environmental drivers of the taxonomic, functional, and phylogenetic diversity of small mammals in a karst mountain area. *Ecology and Evolution* 10: 10899–10911. <https://doi.org/10.1002/ece3.6750>
- Swenson NG, Enquist BJ, Thompson J, Zimmerman JK (2007) The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770–1780. <https://doi.org/10.1890/06-1499.1>
- Tan YB, Shen WH, Fu Z, Zheng W, Ou ZY, Tan CQ, Peng YH, Pang SL, He QF, Huang XR, He F (2019) Effect of environmental factors on understory species diversity in Southwest Guangxi *Excentrodendron tonkinense* forests. *Biodiversity Science* 27: 970–983. <https://doi.org/10.17520/biods.2019133>
- Tietje M, Antonelli A, Forest F, Govaerts R, Smith SA, Sun M, Baker WJ, Eiserhardt WL (2023) Global hotspots of plant phylogenetic diversity. *The New Phytologist* 240: 1636–1646. <https://doi.org/10.1111/nph.19151>
- Vamosi SM, Heard SB, Vamosi JC, Webb CO (2009) Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18: 572–592. <https://doi.org/10.1111/j.1365-294x.2008.04001.x>
- Wang B, Huang YS, Li XK, Xiang WS, Ding T, Huang FZ, Lu SH, Han WH, Wen SJ, He LJ (2014) Species composition and spatial distribution of a 15 ha northern tropical karst seasonal rain forest dynamics study plot in Nonggang, Guangxi, southern China. *Biodiversity Science* 22: 141–156. <https://doi.org/10.3724/sp.j.1003.2014.13195>
- Watanabe S, Maesako Y, Inada T (2024) Spatial pattern of woody plant species richness and composition in primary warm temperate evergreen forest in Kasugayama Hill, Japan. *Scientific Reports* 14(1): 26570. <https://doi.org/10.1038/s41598-024-77438-y>
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150448>
- Weigel R, Gilles J, Klisz M, Manthey M, Kreyling J (2019) Forest understory vegetation is more related to soil than to climate towards the cold distribution margin of European beech. *Journal of Vegetation Science* 30: 746–755. <https://doi.org/10.1111/jvs.12759>
- Weintraub SR, Taylor PG, Porder S, Cleveland CC, Asner GP, Townsend AR (2015) Topographic controls on soil nitrogen availability in a lowland tropical forest. *Ecology* 96: 1561–1574. <https://doi.org/10.1890/14-0834.1>
- Wu Y, Yang Q, Wen Z, Xia L, Zhang Q, Zhou H (2012) What drives the species richness patterns of non-volant small mammals along a subtropical elevational gradient? *Ecography* 36: 185–196. <https://doi.org/10.1111/j.1600-0587.2011.07132.x>
- Xiao YM, Yang LC, Nie XQ, Li CB, Xiong F, Wang LL, Zhou GY (2019) Effects of slope position on phylogenetic diversity and structure of alpine shrub community. *Shengtaixue Zazhi* 38: 1611–1619.
- Yan W, Zhou Q, Peng D, Luo Y, Chen M, Lu Y (2022) Response of surface-soil quality to secondary succession in karst areas in Southwest China: Case study on a limestone slope. *Ecological Engineering* 178: 106581. <https://doi.org/10.1016/j.eco-leng.2022.106581>



- Yang J, Zhang GC, Ci XQ, Swenson NG, Cao M, Sha LQ, Li J, Baskin CC, Slik JWF, Lin LX (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. *Functional Ecology* 28: 520–529. <https://doi.org/10.1111/1365-2435.12176>
- You GY, Zhang YP, Liu YH, Schaefer D, Gong H, Gao JB, Lu ZY, Song QH, Zhao JB, Wu CS, Yu L, Xie YN (2013) Investigation of temperature and aridity at different elevations of Mt. Ailao, SW China. *International Journal of Biometeorology* 57: 487–492. <https://doi.org/10.1007/s00484-012-0570-6>
- You YM, Xu JY, Cai DX, Liu SR, Zhu HG, Wen YG (2016) Environmental factors affecting plant species diversity of understory plant communities in a *Castanopsis hystrix* plantation chronosequence in Pingxiang, Guangxi, China. *Acta Ecologica Sinica* 36: 164–172. <https://doi.org/10.5846/stxb201411242332>
- Yu M, Zhou ZY, Kang FF, Ouyang S, Mi XC, Sun JX (2013) Gradient analysis and environmental interpretation of understory herb-layer communities in Xiaoshegou of Ling-kong Mountain, Shanxi, China. *Acta Phytocologica Sinica* 37: 373–383. <https://doi.org/10.3724/SP.J.1258.2013.00039>
- Yuan S, Yue Y, Zhang X, Wang L, Zhai L, Wang K (2024) Human disturbance exacerbated erosion and deposition in the karst peak-cluster depressions during the Ming and Qing dynasties. *Science China. Earth Sciences* 67: 3550–3561. <https://doi.org/10.1007/s11430-023-1406-y>
- Zanne AE, Tank DC, Cornwell WK, Eastman JM, Smith SA, FitzJohn RG, McGlinn DJ, O’Meara BC, Moles AT, Reich PB, Royer DL, Soltis DE, Stevens PF, Westoby M, Wright IJ, Aarssen L, Bertin RI, Calaminus A, Govaerts R, Hemmings F, Leishman MR, Oleksyn J, Soltis PS, Swenson NG, Warman L, Beaulieu JM (2014) Three keys to the radiation of angiosperms into freezing environments. *Nature* 506: 89–92. <https://doi.org/10.1038/nature12872>
- Zeng WH, Shi W, Tang YS, Zheng WY, Cao KF (2018) Comparison of the species diversity and phylogenetic structure of tree communities in karst and non-karst mountains in Guangxi. *Acta Ecologica Sinica* 38: 8708–8716. <https://doi.org/10.5846/stxb201808021643>
- Zeng X, Li ZG, Liu SY, Chao L, Wang AH, Su HX, Mao B, Liu YY (2023) Analyses on functional characteristics of hydraulic architecture of nine main tree species in karst forest in Nonggang of Guangxi and their correlations. *Journal of Plant Resources and Environment* 32: 52–60.
- Zeng XH, Zhang WJ, Song YG, Shen HT (2014) Slope aspect and slope position have effects on plant diversity and spatial distribution in the hilly region of Mount Taihang, North China. *Journal of Food Agriculture and Environment* 12: 391–397.
- Zeng ZX, Wang KL, Liu XL, Zeng FP, Song TQ, Peng WX, Zhang H, Du H (2015) Stoichiometric characteristics of plants, litter and soils in karst plant communities of Northwest Guangxi. *Acta Phytocologica Sinica* 39: 682–693. <https://doi.org/10.17521/cjpe.2015.0065>
- Zhang H, Zhu Y, Han T, Ren Y, Yu S (2024) Optimization of conservation network based on phylogenetic diversity—A case of some vascular plants on the Qinghai-Tibet Plateau. *Biodiversity and Conservation* 33: 2089–2108. <https://doi.org/10.1007/s10531-024-02846-5>
- Zhang J (2018) Plantlist: looking up the status of plant scientific names based on the plant list database. R package version 0.5.3. <https://github.com/helixcn/plantlist/> [Accessed 9 June 2020]



- Zhang QW, Zhu SD, Jansen S, Cao KF (2021) Topography strongly affects drought stress and xylem embolism resistance in woody plants from a karst forest in Southwest China. *Functional Ecology* 35: 566–577. <https://doi.org/10.1111/1365-2435.13731>
- Zhang R, Yu FY, Zhou RH, Dong HJ, Wang M, Ye X, Hao JF (2020) Effects of slope position and aspect on structure and species diversity of shrub community in the Jiajin Mountains, Sichuan Province, China. *Ying Yong Sheng Tai Xue Bao* 31: 2507–2514. <https://doi.org/10.13287/j.1001-9332.202008.004>
- Zhang WX, Huang DZ, Wang RQ, Liu J, Du N (2016) Altitudinal patterns of species diversity and phylogenetic diversity across temperate mountain forests of northern China. *PLOS ONE* 11: e0159995. <https://doi.org/10.1371/journal.pone.0159995>
- Zhang ZH, Hu G, Zhu JD, Ni J (2013) Aggregated spatial distributions of species in a subtropical karst forest, southwestern China. *Journal of Plant Ecology* 6: 131–140. <https://doi.org/10.1093/jpe/rts027>
- Zhu L, Jin YL, Cong RH, Liu QF, Ding Y, Zhang Q (2018) Effects of environmental factors and interspecific competition in community biodiversity pattern. *Ganhanqu Yanjiu* 35: 1427–1435.

## Supplementary material 1

### Environmental variables along the slope position gradient in a karst peak-cluster depression landform

Authors: Qingling Pang, Cong Hu, Chaohao Xu, Chaofang Zhong, Zhonghua Zhang, Gang Hu  
Data type: docx

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/natureconservation.60.162595.suppl1>